The ewe N778 was placed with rams in two successive breeding seasons and, if bred, never conceived. Although superficially she would have passed as a normal ewe, examination of her vagina indicated that she was very probably a freemartin. She was killed and examined by veterinarians on the staff of the School of Veterinary Medicine. Although the anatomical details of this examination are not given in this report, they left no doubt that N778 was a true freemartin.

Our data in conjunction with Lillie's and Rotermund's would suggest an approximate frequency of placental anastomosis of 5% in sheep twins. Given about one birth in three a twin birth and a sex ratio of approximately one pair of heterosexual twins to every pair of like-sexed twins (8), this would lead to estimating the frequency of freemartins among ewes as about 0.8%. This estimate is undoubtedly too high. Nevertheless, while the frequency of freemartinism might be low enough to escape detection by breeders, particularly if it is generally somewhat cryptic, as in the case of N778, it might nevertheless be frequent enough to explain a significant portion of nonbreeders among ewes. We are convinced that freemartinism would have gone undetected in the case of N778 had it not been for the observation of erythrocyte mosaicism.

References

- OWEN, R. D. Science, 102, 400 (1945).
 OWEN, R. D., DAVIS, H. P., and MORGAN, R. F. J. Heredity, 37, 291 (1946).
- 3. STORMONT, C., LANE, L. L., and WEIR, W. C. In preparation.
- 4. LILLIE, F. R. J. Exptl. Zool., 23, 371 (1917).
- 5. ROBERTS, J. A. F., and GREENWOOD, A. W. J. Anat., 63, 87 (1928).
- 6. EWEN, A. H., and HUMMASON, F. A. J. Heredity, 38, 149 (1947).
- 7. ROTERMUND, H. Tierärztl. Hochsch. Hannover (1929).
- 8. MARSHALL, F. R., and POTTS, C. G. U. S. Dept. Agr. Bull., 996, 8 (1921).

Manuscript received September 2, 1953.

Photosynthesis as a Photoelectric Phenomenon

Leonard S. Levitt Department of Chemistry. Stevens Institute of Technology, Hoboken, New Jersey

The purpose of this paper is to propose a new mechanism for the crucial step of quantum conversion in photosynthesis. Quite recently it has been established that the prosthetic group of pyruvic acid oxidase is 6,8-thioctic acid (which may be abbreviated carbon dioxide is not absorbed into the cycle in the presence of light, it is thought that the disulfide group of pyruvic oxidase must be unavailable during the light reaction of photosynthesis.

It was proposed (1, 2) that the chlorophyll molecule absorbs a quantum of red light and transfers the electromagnetic energy to the already strained disulfide ring, resulting in its dissociation to a dithiyl radical $RCH-CH_2-CH_2-S$ which was then presumed to Ś٠

extract two hydrogen atoms from some other molecule, possibly water (3), yielding the reduced dithiol RCH-CH₂-CH₂-SH.

SH

To the author it appears rather unlikely for free radicals of any type to be produced within a living cell in aqueous solution (or suspension) where ions can be formed by means of a considerably smaller expenditure of energy. The transfer of electrons can occur much more rapidly and efficiently than the transfer of relatively cumbersome hydrogen atoms, and it is not to be supposed that nature has not yet been apprised of the fact. Thus, the direct capture of two electrons by the disulfide group of pyruvic oxidase would result immediately in the reduced dithiol state:

$$\begin{array}{cccc} \operatorname{RCH}-\operatorname{CH}_{2}-\operatorname{CH}_{2} & \operatorname{RCH}-\operatorname{CH}_{2}-\operatorname{CH}_{2}-\operatorname{S}:^{-} \\ & & & & & \\ & & & \\ & & & & \\ & & & & \\ & & & \\ & & & \\ & & & \\ & & & \\ & & & \\ & & & \\ & & & \\ & & & \\ & & & \\ & & & \\ & & & \\ & & & \\ & & & \\ & &$$

In such an event there would be no need to search further for "the precise species from which the sulfurfree radicals snatch the hydrogen" (2). All that is needed to complete the molecule, if, indeed, it is in need of completion, is two protons, which, in any aqueous system, are readily available.

There is some evidence (3) that the reduction product of the disulfide may sometimes be a thiol sulfenic acid of the type RSSH. In that case the C-S bond is broken instead of the S-S bond, and the immediate reduction product after the electron transfer would be RCH-CH₂-CH₂-S-S:

If the idea of electron transfer be accepted, the only question remaining would be "whence the two electrons?" A logical answer might be as follows: the chlorophyll molecule, on bombardment with photons of red light, absorbs one quantum, resulting in the activation of an electron to such a high-energy level that it is easily extracted by a mild oxidizing agent intimately associated with the chlorophyll molecule, namely, the disulfide group of pyruvic oxidase.

Probably the most fundamental reaction in photosynthesis is the oxidation of water:

$$H_2O \longrightarrow \frac{1}{2}O_2 + 2H^+ + 2e^-$$
 (2)

Now, instead of assuming (4) that chlorophyll in some way transfers its absorbed electromagnetic energy to a water molecule, which subsequently decomposes in the presence of a suitable oxidizing agent, let us assume again that chlorophyll molecules, on bombardment with photons, transfer electrons to the disulfide

 $RCH-CH_2-CH_2-S-S$, and that it is the disulfide (oxidized) form of this substance that is required in order that the oxidative decarboxylation of pyruvic acid take place (1, 2). It has been observed also that the presence of this compound is necessary in order that carbon dioxide be incorporated into the Krebs cycle to occur during photosynthesis (1, 2). Since

and extract electrons from a water molecule. Therefore, while the oxidation of water is proceeding in the light, the incorporation of carbon dioxide into the tricarboxylic acid cycle is inhibited by the unavailability of the disulfide.

Whether or not chlorophyll exists intermediately as an ephemeral ionic species in this scheme depends only on the time lag between the initial loss of an electron by the chlorophyll molecule and the subsequent recapture of an electron from a water molecule. If the time lag is relatively great, then the chlorophyll will have been oxidized to a relatively long-lived positively charged ion. If the time lag is extremely small, as it would be if the new electron is acquired to replace the one removed from its normal energy level simultaneous with, or even before, the loss of the activated electron, then oxidative ionization of chlorophyll will not have taken place. In this connection, Rabinowitch (5), taking into account the absorption and fluorescence spectra and the photo-oxidation of chlorophyll in the presence of electron-accepting ions and molecules, states "Indications (are) that the activated chlorophyll molecules which fail to emit fluorescence are converted into a long-lived active form which may represent . . . an oxidized or reduced molecular species."

According to the present theory, then, the mechanism of photosynthesis may be summed up by the following equations:

$$\operatorname{Chl} + h_{\mathcal{V}} \longrightarrow \operatorname{Chl}^*$$
 (3)

$$2 \text{Chl}^* + \text{RSSR} \longrightarrow 2 \text{Chl}^+ + 2 \text{RS}^-$$
 (4)

$$2\mathrm{Chl}^{+} + \mathrm{H}_{2}\mathrm{O} \longrightarrow 2\mathrm{Chl} + 2\mathrm{H}^{+} + \mathrm{O}$$
 (5)

in which Chl* and Chl+ represent chlorophyll with, respectively, an activated electron and a missing electron.¹ It will be noted that four quanta are required for the production of one oxygen molecule according to this scheme.

Equations 4 and 5 may be combined to indicate the possible simultaneity of these two reactions:

$$2\mathrm{Chl}^* + \mathrm{RSSR} + \mathrm{H}_2\mathrm{O} \longrightarrow 2\mathrm{Chl} + 2\mathrm{RS}^- + 2\mathrm{H}^+ + \mathrm{O} \quad (6)$$

This may, perhaps, be best represented in typical biochemical notation for coupled reactions:



The entire process may thus be visualized as a flow of electrons actuated by light; or, essentially, as a photoelectric current flowing from water through the chlorophyll to the disulfide. The light-activated chlorophyll molecule, according to this view, appears to play the role of an oxidation-reduction enzyme (a dehydrogenase) and functions almost as what might be described as a conducting bridge between two half-cells in which reactions 1 and 2 are, respectively, taking place.

References

- 1. CALVIN, M. Chem. Eng. News, 31, 1622 (1953).
- -. Ibid., 1735 (1953).
- *Ibid.*, 3550 (1953).
 GRANICK, S. *Ibid.*, 748 (1953).
 RABINOWITCH, E. *Photosynthesis*. New York : Interscience Pub., p. 754, 1951.

Manuscript received September 11, 1953.

Tolerance of Certain Higher Plants to Chronic Exposure to Gamma Radiation from Cobalt-60¹

Arnold H. Sparrow and Eric Christensen

Biology Department, Brookbaven National Laboratory, Upton, New York

Although the tolerance of a considerable number of species of higher plants to acute doses of ionizing radiation is known, only a few reports are available concerning tolerance of growing plants to chronic exposure to ionizing radiation. For this reason, a summary of preliminary information is presented here relating to the influence of chronic gamma radiation from cobalt-60 on a wide range of different species.

The Co⁶⁰ sources used varied in strength from about 8 to 1800 curies, and the investigations were conducted under both greenhouse and field plot conditions. The procedure used for growing and irradiating the different species was that previously described by Sparrow and Singleton (1).

Under the conditions of our experiment, cytological, genetic, and physiological effects are known to occur (1, 2). However, the criterion used here to evaluate the effect of the radiation is the gross morphological appearance of the plant. In general, a mild effect means a slight decrease in height or vigor of the plant, and a severe effect means a definite, often dramatic. deviation from the normal or control plant in size. vigor, and in many cases general morphology (3, 4). Thus, in most cases, a "severe effect" means acute stunting or dwarfing from which the plant might or might not recover.

As shown in Table 1, there are considerable differences in the tolerance of different species to chronic irradiation. Certain plants (Tradescantia paludosa and Lilium longiflorum) show a mild effect at a dose rate of about 20 r/day, while others (broccoli and gladiolus) show no definite effects at dosages lower than 1400 and 4100 r/day, respectively. These data indicate a 200-fold difference in sensitivity between the least tolerant and most tolerant species so far investigated. A similar range is also shown by comparing the dose rate required to produce a severe effect

December 4, 1953

¹The coefficient 2 before Chl* is not to be construed as indicating that photosynthesis necessarily is kinetically second order with respect to activated chlorophyll, since the two-electron transfer may actually occur in two more or less distinct steps, rather than simultaneously.

¹ Research carried on at Brookhaven National Laboratory ander the auspices of the U.S. Atomic Energy Commission.